ground water

Ecological Consequences of Ground Water Discharge to Delaware Bay, United States

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Abstract

Submarine ground water discharge to the ocean has the potential to create estuarine conditions near the point of discharge, thereby dramatically altering local benthic habitats and ecology. Aerial thermal infrared imaging along the southwestern margin of Delaware Bay indicated abundant discharge at Cape Henlopen, Delaware, adjacent to the Atlantic Ocean. On the sandflat there, we have documented low salinity in sedimentary pore waters within 20 m of the beachface that are associated with dense assemblages (in thousands per square meter) of a deep, burrow-dwelling polychaete worm, *Marenzelleria viridis*, otherwise regarded as a species characteristic of fresher, oligohaline conditions. Where present, *M. viridis* is a numerical and biomass dominant in a benthic community strikingly different from that in nearby nonseep locations. At Cape Henlopen, the ecological role of the ground water discharge appears to be a multifaceted one. Seeps are localized regions of significantly reduced salinity, stabilized temperature, increased nutrient flux, high microalgal abundance, and enhanced sediment stability. *M. viridis* feeds on sediment diatoms and may provide an important trophic linkage between microalgal growth fueled by nutrients associated with the discharging ground water and worm-feeding predators such as bottom fish or shorebirds common on the Cape Henlopen sandflat. Calculations based on our sampling suggest that nutrients supplied by the ground water substantially exceed what is needed to support benthic biomass and productivity estimated for this site.

Introduction

Submarine ground water discharge to the oceans and estuaries is a widely recognized phenomenon (Garrels and Mackenzie 1971; Zektzer et al. 1973), and recent estimates suggest that ground water contributes 10%, perhaps significantly more, of the total fresh water flux to the coastal environment (Zektzer and Loaiciga 1993; Moore 1996). These seepage zones have been termed subterranean estuaries (Moore 1996, 1999) because they represent regions of mixing of fresh and salt waters. However, since discharged ground water is often enriched in nutrients relative to marine and surface waters, seepage may be a far more important source of nutrients than the flux of water alone suggests (Valiela et al. 1992; Moore 1996, 1999; Li et al. 1999; Shaw 2001; Burnett et al. 2002).

While ground water seeps have been best studied for their hydrology and sedimentary biogeochemistry (Reay et al. 1992; Valiela et al. 1990; Uchiyama et al. 2000), these zones also represent small-scale estuarine features in terms of biological habitat and the species that inhabit them (Kohout and Kolipinski 1967; Johannes 1980; Johannes and Hearn 1985; Bussman et al. 1999). Seeps present a unique, yet localized, habitat that allows specialized estuarine species to exist in a marine setting and thus contribute to overall biodiversity. Because of high nutrient input and specially adapted organisms, seeps may be hot spots of biological productivity and trophic transfer from algae at the base of the food web, through grazers and detritivores, to predatory invertebrates, fish, and shorebirds. Productivity in the seepage zones may thus drive enhanced transfer of ground water-borne nutrients, and possibly contaminants, through to various levels of marine and avian food chains.

The purpose of this paper is to describe the potential ecological roles of submarine ground water discharge at Cape Henlopen, Delaware Bay, United States. This site was first recognized as a seep zone from the unusual and abundant benthic community on restricted regions of the sandflat there. Subsequently, we conducted an aerial thermal

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infrared survey that identified other nearby seepage zones. In this paper, we present the results of the thermal survey and on-site characterization of the seepage zone, and document the benthic community and trophic relationships (i.e., food web) found there. Based on our preliminary measurements and literature values, we speculate on the role of ground water nutrient discharge in supporting the high biomass and productivity we have observed at this site. We suggest that high rates of primary and secondary productivity that we infer from our observations are indeed supportable by ground water-derived nutrients.

Methods

Study Area

Delaware Bay is a large, shallow, coastal plain estuary located on the mid-Atlantic coastline of the United States (Figure 1a). The primary fresh water input is from the Delaware River, and tidal exchange with the ocean maintains a well-mixed water column in the lower Delaware Bay. There is also fresh water inflow from streams along the study area in the southwestern half of the bay, including the St. Jones, Murderkill, Mispillion, and Broadkill rivers, and Cedar, Slaughter, Primehook, and Mill creeks (NOAA 1985). These streams have contributed extensively to reworking of the shoreline and the heterogeneity of bay-margin sediments. The shoreline itself consists of barrier beaches, headlands, and salt marshes landward of the beach. Relict marsh sediments crop out at several locations within the study region (Kraft 1971; Honeycutt 1997).

Cape Henlopen is a large beach spit complex located at the intersection of Delaware Bay and the Atlantic Ocean (Figure 1b). The cape is an active feature characterized by the erosion of its Atlantic margin, its propagation northward toward New Jersey, and the infilling of the intertidal zone behind the propagating spit (Maurmeyer 1974). There are a number of cycles of beach ridges and dunes associated with

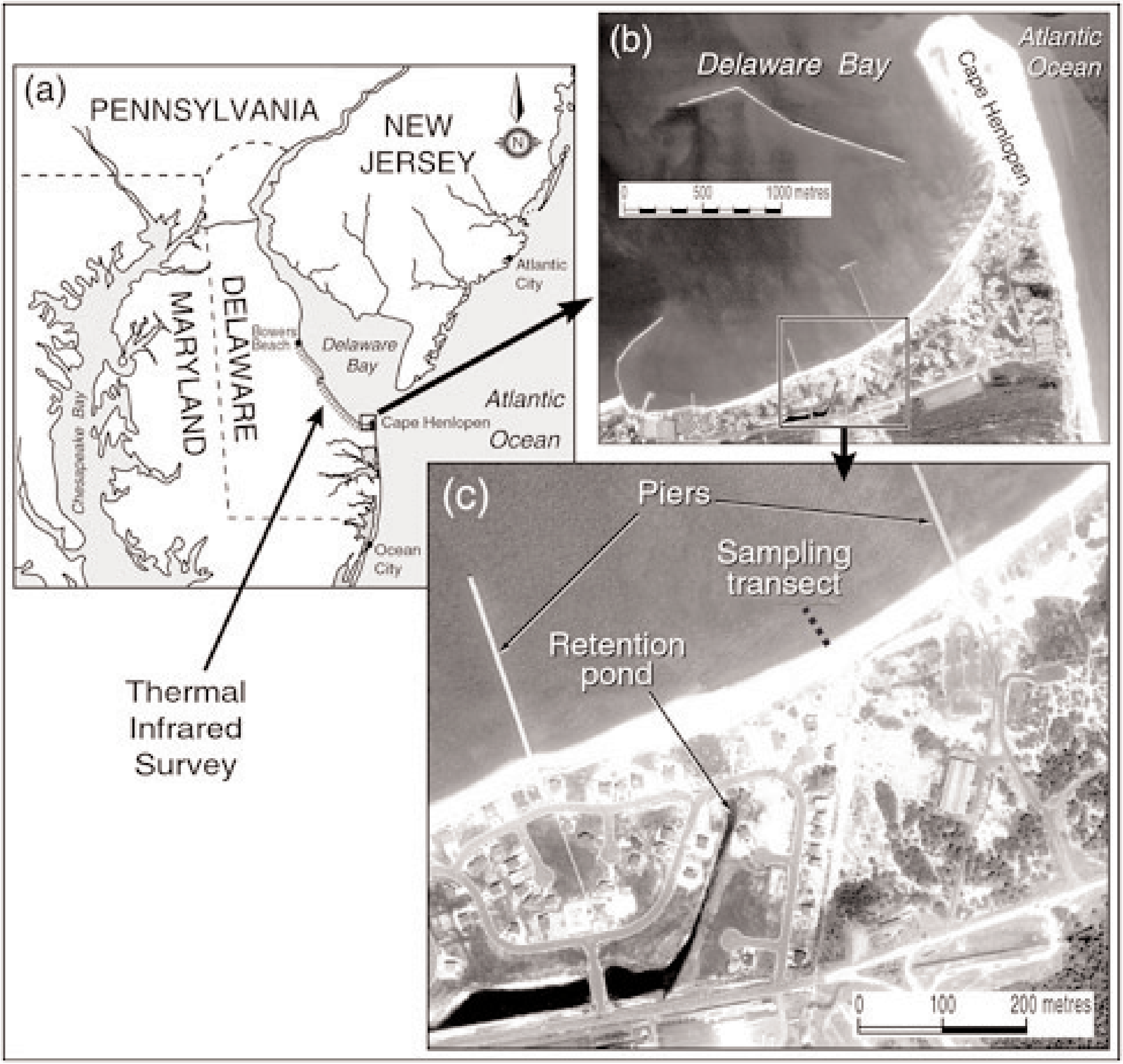

Figure 1. Location of study site and pore water survey: (a) Delaware Bay and aerial thermal survey along southwestern margin of bay; Cape Henlopen aerial orthophotos (1997) showing (b) Cape Henlopen, shoreline, piers, and breakwater, and (c) location of the monthly sampling transect.

the Pleistocene, Holocene, and modern evolution of the complex (Kraft 1971). The estuarine waters at Cape Henlopen are well mixed and typically have salinities similar to that of the local coastal ocean (salinity S = 25 to 30) (Kawabe et al. 1988; Muir 2002). There are seasonal patterns of nutrient concentrations in the estuarine waters reflecting nutrient discharges from the Delaware River and estuarine biogeochemistry (Sharp et al. 1982). Wide sandflats behind the cape are exposed at low tide (Figures 1b and 1c) and inhabited by a previously studied benthic community (Ray 1989; Miller et al. 1992; Bock and Miller 1994, 1995; Karrh and Miller 1996). Because of our prior experience and ready access to the site, the Cape Henlopen sandflats were the focus of pore water and biological sampling.

Thermal Imaging

On March 21, 1999, a thermal infrared survey of the southwestern margin of Delaware Bay was conducted before sunrise from a low-flying aircraft in order to map the extent of ground water seepage at this and adjacent sites. Oblique thermal infrared imagery was collected by Aero-Marine Services (Groton, Connecticut) from Cape Henlopen to Bowers Beach, Delaware (Figure 1a), which is a straight-line distance of 38 km. Imagery was collected using a Texas Instruments RS 310 high-resolution thermal mapping system. In two passes over the study area during a predawn low-tide period, overlapping images were taken along the entire shoreline at ~1 m resolution. Our survey was conducted at a time when air temperatures were near 0^oC, and surface estuarine water temperatures were $\sim 5^oC$. Both air and bay water temperatures are well below that of ground water at this time of the year, between 8^o and 12^oC, with the temperatures increasing with depth (Wehmiller et al. 2000). Seepage zones would be warmer by several degrees and appear as hot spots in our thermal survey (Banks et al. 1996; Portnoy et al. 1998). This interpretation of the thermal imagery was confirmed at the previously recognized, extensive seeps at Cape Henlopen, and this site was chosen for more detailed hydrogeochemical sampling (Ullman et al. 2003). Thermal anomalies elsewhere in the survey were also investigated to assess the distribution of seepage locations and their relation to shoreline features and geology.

Sandflat Sampling

Sampling at the Cape Henlopen, Delaware, sandflat (38°47.2′N, 75°06.1′W) within Breakwater Harbor was initiated in January 1996 and continued monthly through January 1999. Within the harbor, large sandflats are exposed along 2.3 km of shoreline and extend an average of 100 m from the beachface at maximum tidal exposure. The nominal spring tidal range is 1.5 m (Polis and Kuferman 1973), and spring tides allowed sampling once or twice each month year-round. All sampling was conducted at times of low tide when the sandflat was exposed as sandbars and tide pools with water, and at or below the 0.0 m mean lower low water (MLLW) tidal datum.

To provide a fixed frame of reference on the sandflat for repeated sampling at monthly intervals, a transect was established at 38°47.158′N, 75°06.215′W, ~180 m west/southwest of the fishing pier near the western boundary of Cape Henlopen State Park (Figure 1c) in January 1996. This monthly transect of 16 posts, located 1 m apart, extended from the base of the beachface seaward, perpendicular to the shoreline, and across known patches of the *Marenzelleria viridis*. To avoid any flow, sediment, or faunal disturbances, posts were used for location purposes only; the exact locations for well placement and pore water sampling were unmarked, 1 m east of the line of posts. Sixteen pore water samples were taken approximately monthly at spring low tides during the first year and a half of the study. In July 1997, this transect was extended across the first tide pool to a sandbar crest. These eight additional sampling posts and well sample points (also each 1 m apart perpendicular to the shoreline for a total of 24 in all) allowed us to sample from the *M. viridis* patches to a different benthic community characterized by species such as *Spiochaetopterus oculatus* (Bock and Miller 1995). In a separate effort to gauge variability along the shoreline at Cape Henlopen, 13 additional temporary transects were established in July 1996. Along a 3 km stretch of the shoreline in Breakwater Harbor, 150 m apart both east and west of the main transect, pore water samples were taken at 2 m intervals from the base of the beach to 10 m offshore. This one-time sampling effort will be denoted as the harbor transects.

We obtained pore water samples using small piezometers, henceforth termed wells, pushed into the sediment. These wells were constructed from conical-tipped, 50 mL polypropylene tubes (3 cm diameter) extended vertically using 20 cm lengths of 1.9 cm PVC pipe secured with black tape. When pushed into the sediment to a depth of 8 to 10 cm, wells filled by gravity through five 2.5 mm diameter holes drilled in the conical tube bottoms. To avoid mixing with water from the surface or other depth, it was routine to discard the first fill of the well and retain the second for analysis. Conductivity of the samples was determined to 0.1 mS/cm (temperature corrected to 25^oC) in the laboratory using a conductivity meter (Cole-Parmer Model 1481–40) calibrated before each use and converted to salinity by the equation $S = 0.4081 \times C^{1.121}$ (Riley and Skirrow 1975).

On four occasions, in June and September 1997, and January and March 1998, we obtained cores for benthic macrofauna along the same transect as sampled for pore waters. Due to time and tide limitations, two low tides were generally required to sample the entire transect. Cores were 5.4 cm diameter plastic tubes, pounded into the sediment, and dug out by hand to a depth of 30 cm. Cores were taken ~1 m east of the transect, but randomly offset 0.2 or 0.4 m to avoid coring previously sampled sediments. To obtain an undisturbed pore water sample for each macrofauna core, a well was inserted adjacent to each core, and the pore water sample taken as described previously prior to removal of the cores from the sediment. Sediment was field sieved on a 1 mm mesh to retain macrofauna, which were subsequently preserved in formalin, washed, and stored in alcohol. Organisms were identified under a dissecting microscope and enumerated with abundances normalized for the 22.9 cm^2 core area.

Results

Thermal Imagery and the Distribution of Ground Water Discharge

The March 1999 thermal infrared survey indicated ground water seepage in many areas along the southwestern coastline of Delaware Bay, with the highest levels appearing near Cape Henlopen. Twenty-one thermal anomaly sites were identified from the aerial survey and visited during the following summer and fall. Many of the observed anomalies are evidently due to the seepage of warmer and saline marsh waters across a narrow barrier beach, while others appear to be the result of discharge of salt water that had infiltrated the beachface during the previous high tide period. At Cape Henlopen (Figure 2), fresh water seepage is widespread and associated with the previously known *M. viridis* areas between the piers and extending to the east (Ray 1989; Bock and Miller 1994, 1995). We confirmed ground water discharge with field observations of diluted tide pool and pore water salinity (as follows). The Cape Henlopen barrier beach spit complex is sufficiently porous and large enough to sustain a local fresh water table (Sharp 1980). Overall, direct ground water seepage to the estuary elsewhere along the southwestern margin of Delaware Bay was rare. While thermal anomalies were present in creeks, generally none was seen on nearby beachfaces. We investigated several thermal anomalies seaward of marshes, and at these sites found neither reduced salinity nor other evidence of fresh water discharge. Our interpretation is that any direct ground water seepage from the uplands is intercepted by tidal creeks in the salt marshes behind the barrier beaches. This water is then discharged to the bay through surface pathways rather than as direct seepage through the beachface.

At Cape Henlopen, the zones along the beachface with the most extensive areas of high-temperature anomalies, and the highest apparent seepage rates, were found to be adjacent to a new housing development behind Cape Henlopen (Figures 1c, 2a, and 2b). These seeps appear to be associated with the historical positions of a tidal creek that has been converted into a storm water retention pond for the Cape Shores development. Although the maximum seepage appears to be associated with the former position of a creekbed, thermal infrared evidence of seepage was found several hundred meters either side of this point (Figures 2a and 2b).

Sandflat Sampling of Seepage Sites at Cape Henlopen

Figure 3a shows pore water salinity along the monthly transect across the seep zone located 180 m west/southwest of the fishing pier in March 1996, March 1997, March 1998, and January 1999 for comparison with the thermal overflight results. These salinity profiles show two regions of lowered salinity, below 20 and as low as 5, between 6 to 9 m and 12 to 15 m. Salinities near the beachface, at 10 to 11 m midtransect and at the offshore end (> 20 m out), show high salinities near 25. Delaware Bay water at Cape Henlopen is euhaline, salinity ranging seasonally from ~25 to 30, with lowest values in spring and highest in fall (Kawabe et al. 1988; Muir 2002). Sampling this transect at monthly intervals over these three years (37 samplings of 16 or 24 points) shows this same spatial pattern for winter samples as well as repeatable seasonal variations (Figure 3b). In the winter and spring of each year, low pore water salinities (half-strength sea water or less) were found in two patches located 6 to 9 m and 12 to 14 m from the beach (Figure 3b). Lowered salinities are found in the 6 to 9 m region throughout the year, while the 12 to 14 m region is freshened only in the spring. The temporal pattern of freshest pore water in the spring and saltier in the fall repeats in each of the three years sampled (Figure 3b), consistent with the hydrological expectation that discharge will be at a maximum when seasonal evapotranspiration is at a minimum.

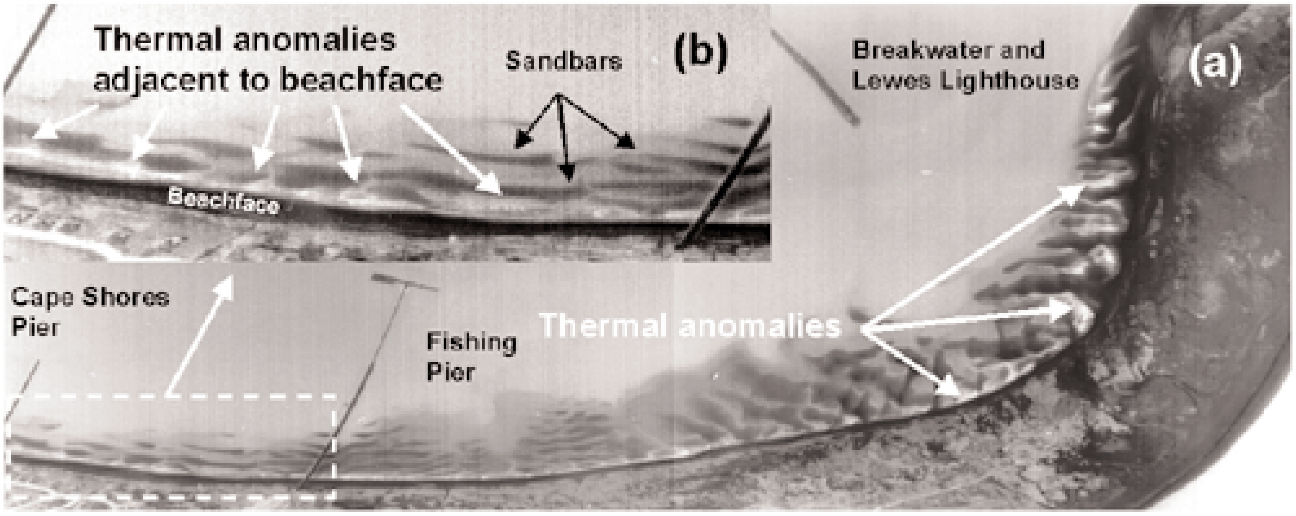

Figure 2. Oblique thermal images (a) between Cape Henlopen and the piers (corresponding to Figure 1b), and (b) inset of sandflat between the piers (in Figure 1c). Ground water seepage is visible as lighter (warmer) areas bayward of the dark (cooler) beachface and amidst topographically higher (but cooler and dark) sandbars parallel to shore. The images are oblique and not geo-referenced, but for approximate scale, the straight-line distance between Cape Shores and fishing piers is 560 m.

To quantify variations in seepage along the shoreline of Cape Henlopen in July 1996, we measured pore water salinities at 13 harbor transects around Breakwater Harbor, extending relative to the fishing pier 650 m west to 1150 m east, halfway to the tip of Cape Henlopen. Low salinity pore water (S < 20, and as low as S = 5) was found on each of these transects and at variable distances from the beach. These data demonstrate that seepage is widespread at Cape Henlopen although there is much spatial variability, a distribution consistent with that derived from thermal imaging (Figure 2b). It is important to note the harbor transect sampling occurred at a time of minimal discharge at the main transect (Figure 3b).

Benthic Macrofauna and Microflora

The association of low salinity regions and certain benthic macrofauna was quite apparent visually in the seepage zone. The red gilled mud worm, *M. viridis*, is a large, deep-burrowing deposit-feeder that defecates pellets as long strings of sediment. When in high abundance, actively feeding worms cover the sediment surface with pellets that reveal the location and horizontal extent of dense patches of the worms. Pore water sampling of these fecal pellet patches consistently showed reduced pore water salinity in and near worm patches (Miller 1996 unpublished observations).

To quantify this association, we sampled the benthic macrofaunal community along the salinity transect at four seasonal time points in 1997 and 1998, and found red gilled mud worm populations present year-round. Highest abundances (many thousands per square meter) of *M. viridis* are associated with both of the freshened regions 6 to 9 m and 12 to14 m from the beach (Figure 4). Regardless of season (Figures 4a and 4b), high worm abundances are found in salinities generally below 15, and most low or zero abundances are found at salinities above 25. This wedge-shaped scatter of points is the pattern in worm abundances expected for an oligohaline species. In summer and fall cores (Figure 4a), however, note that several points with high worm abundances and high salinity are evident (circled part in Figure 4a). These cores were taken either from the 12 to 14 m, temporary low salinity region or on the periphery of the permanent seep closer to the beach (Figure 3b). These same locations on the sandflat had far fewer worms and mostly much lower salinity (Figure 4b) in the following winter and spring, and evidently the previous winter and spring (Figure 3b). The high summer and fall abundances (Figure 4a) thus likely reflect recruitment of *M. viridis* during the previous spring during low salinity (Figure 3b). Alternatively, active swimming by adults could have resulted in these high abundances subsequent to larval recruitment. The important implication is that the patches of high worm abundance are present seasonally and reflect salinity conditions several months beforehand. In contrast, other deposit and suspension macrofaunal species common on the sandflat largely are absent from the seep zone (within 15 m of the beach) although they are common on the first sandbar 20 to 25 m from shore (description follows) (Bock and Miller 1995; Muir 2002).

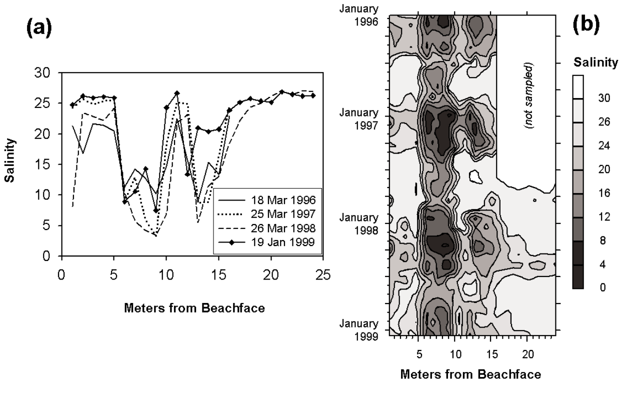

Figure 3. Pore water salinity across the seepage zone: (a) winter and spring transect samples, and (b) contour plot of three-year sampling at pore water salinity transect of either 16 samples (January 1996–July 1997) or 24 samples (August 1997–January 1999) at 1 m intervals from the beachface. A grayscale bar at right represents contoured salinity values.

Another notable characteristic of the benthic ecology of the Cape Henlopen sandflat is the presence of microalgal mats that are especially visible in the late summer and fall (Figure 5). Sediment diatom and cyanobacterial mats appear in the late summer in the seep zone and adjacent tide pools. These microalgal mats discolor the sediment surface and bind the top few millimeters of the sediment into a layer described as a carpet (Miller et al. 1996). The high photosynthetic activity of the algal mat is apparent in the production of bubbles on the carpet's surface. Macroalgae, e.g., sea lettuce (*Ulva*) and hollow-tubed seaweed (*Enteromorpha*), are also found on the sandflat attached to worm tubes, exposed shells, or construction debris (Ray 1989). Their distribution and abundance seems limited by firm substratum for attachment, and macroalgae are only rarely found free-floating.

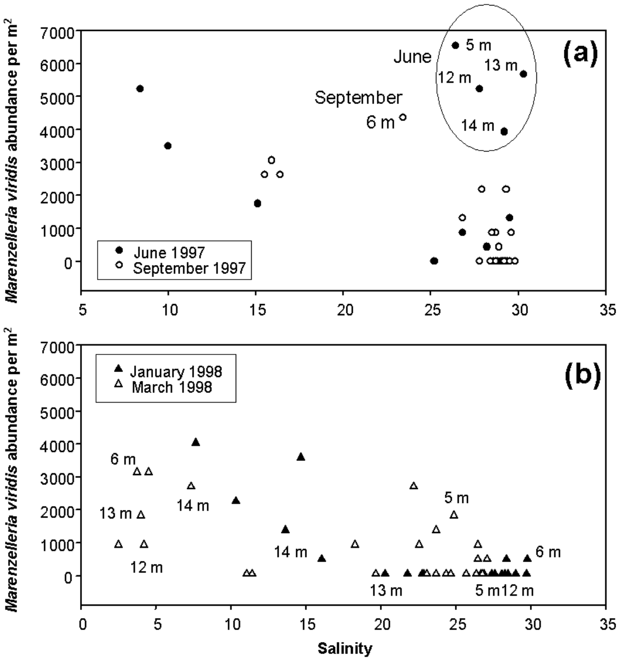

Figure 4. Abundance of *M. viridis* plotted against pore water salinity for four seasonal macrofauna surveys: (a) June and September 1997 cores, and (b) January and March 1998 cores, with samples discussed in text highlighted.

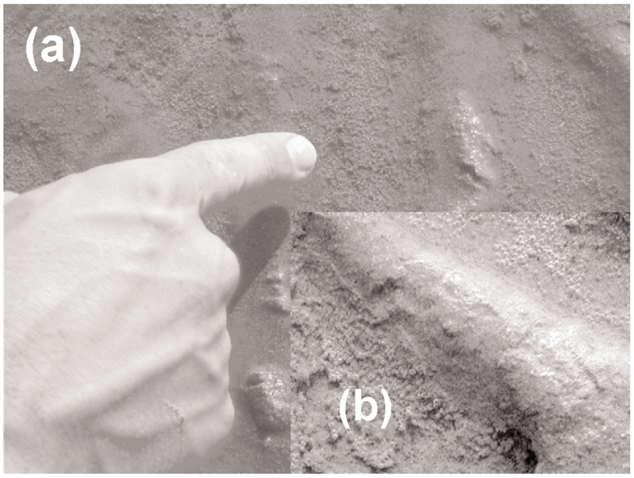

Figure 5. Microalgal mat formed on the (a) sandflat surface, and (b) in close-up view showing numerous bubbles produced by photosynthetic activity of sediment microalgae on both sides of a sand ripple crest (diagonal feature across inset photograph).

Discussion

Characterization of Seeps

Aerial thermal imaging (Figure 2) and on-site pore water sampling (Figure 3) characterized the seeps at contrasting scales, yet both data sets yield a consistent picture of the spatial and temporal variability of seeps in the lower Delaware Bay. Thermal imaging (Figure 2) detected anomalies that were positively associated with ground water seepage at the sandflats in Breakwater Harbor (Figure 2b) and also immediately west of Cape Henlopen (right side of Figure 2a). In both the monthly and harbor transects, seeps were seen only at the beachface and adjacent sandflat (within 10 to 20 m), and along the shoreline there was much variability associated with sandbars and runnels (small troughs formed by beachface seepage, permitting discharge from tide pools across the first sandbar to the bay, ~20 to 30 m from the beachface). At broader scales (tens of meters to kilometers), the patterns of seepage appear to be closely related to shoreline geology, geomorphology, and hydrostratigraphy (Ullman et al. 2003).

Meter- and submeter-scale variability was evident in on-site sampling at the monthly transect (Figures 3a and 3c). Pore water salinities indicate that seepage is far from uniform across the sandflat, with considerable differences in salinity between samples taken a meter apart. Indeed, sampling across worm patches has shown that sharp salinity contrasts can be seen over as little as 10 cm (Miller 1996 unpublished observations). Monthly sampling of the main transect documented seasonal variations in salinity and presumably ground water discharge (Figure 3b). This pattern is consistent with seasonal patterns of precipitation and evapotranspiration and not changes in bay water salinity, which is euhaline year-round at Cape Henlopen.

Note that the thermal imaging was conducted during late winter when we would expect seepage to be near its maximum extent due to seasonally high water tables and low evapotranspiration (Figure 3b). This strengthens our inference that seeps are restricted to the Breakwater Harbor/Cape Henlopen area. In contrast, our 13-transect harbor survey (beachface out 20 m) was conducted during a summer month (July 1996) when we observed strongly reduced seepage at the main transect (Figure 3b). This suggests that seepage at other times of the year may be much more widespread and significant than Figure 2 alone suggests, and this is clearly indicated by the numerous thermal anomalies near Cape Henlopen (Figure 2b) in our late winter thermal survey.

In summary, despite the superficially uniform appearance of the beach, the seeps at Cape Henlopen represent an estuarine habitat restricted to the nearshore regions that is highly fragmented spatially at the 1 to 10 m scale (Figure 3a), yet exhibits a regular seasonal cycle (Figure 3b). Both of these features are of prime importance for the organisms inhabiting the seepage zones.

Benthic Communities Associated with Seeps at Cape Henlopen

M. viridis is a characteristic organism of oligohaline regions of estuaries along the east coast of North America (Dauer et al. 1980; Dauer et al. 1981). While Kinner and Maurer (1978) report its presence in the upper reaches of the Delaware Bay, this species would not be expected to inhabit the euhaline, lower portion near Cape Henlopen. In numerical abundance, individual size, and patchiness of their distribution, our observations from Cape Henlopen agree with those made by others for this species (George 1966; Sardá et al. 1995a, 1995b). Indeed, patchy pelletization of the sediment surface is so characteristic of this species that it was noted in the original, 19th century species description (Verrill 1873). In their tabulation of Cape Henlopen benthic polychaetes, Kinner and Maurer (1978) did not report this species, although this absence probably reflects the highly localized distribution of *M. viridis* as well as their sampling focused on the bars and swales nearer the cape rather than on the sandflat (Maurer and Aprill 1979; Bianchi 1988; Bianchi and Rice 1988). We have observed *M. viridis* present in abundance on the sandflat since at least 1986, and Maciolek (1984) based her description of a new species (*Marenzelleria jonesi*) from this site based on specimens collected in 1977. The synonymy of *M. jonesi* and *M. viridis* has been confirmed by Dauer (1993), and Bick and Zettler (1997), and we will continue to use the latter name.

The close association of *M. viridis* with seeps depicted in Figure 4 is very apparent visually as *M. viridis* are limited to the first flat and trough off the beach, typically within 20 m of the beach slope break where seepage is observed. In the seeps, this single species' abundances may exceed 5000/m^2 as compared with total (i.e., all macrofaunal) abundances of 1300/m^2 at the nearby sandbar (nonseep) areas (Muir 2002). Other benthic species found on the sandbar, as well as interspersed in nonseep areas closer to the beach, include polychaetes such as the glassy tube worm *Spiochaetopterus oculatus*, the mud tube worm *Spio setosa*, the ornamented tube cap worm *Diopatra cuprea*, and a terebellid beard worm *Amphitrite* species. Molluscs include mud snail *Ilyanassa obsoleta*, hard clam *Mercenaria mercenaria*, razor clam *Ensis directus*, and stout razor clam *Tagelus plebius* (Miller et al. 1992). Another notable deposit-feeding species on this sandflat is the acorn worm *Saccoglossus kowalevskii* (Karrh and Miller 1994, 1996).

Muir (2002) concluded that the flat between the beachface and first sandbar was dominated by deposit-feeders (including *M. viridis*), while the sandbar hosted a more trophically mixed community of detritivores, deposit-feeders, and suspension-feeders.

Other benthic organisms play important roles at the base of its food web, and, in particular, sediment diatoms and other microalgae are important primary producers on sandflats (MacIntyre et al. 1996; Miller et al. 1996). From previous studies (Ray 1989; Brandon 1991; Bock and Miller 1995; Karrh and Miller 1994, 1996), we know that values of 10 to 30 μg chlorophyll *a*/gram sediment (where algal biomass is expressed in pigment units) are typical for the Cape Henlopen sandflat in and near the seeps zone, and these agree well with literature values for shallow intertidal sandflats (MacIntyre et al. 1996). For July and August 1987 samples taken across the zone inhabited by *M. viridis* at Cape Henlopen, Ray (1989) reported values of 4 to 15 μg chlorophyll *a*/gram. We have observed that dense microalgal mats appear predictably in late summer, usually in August (Figure 5). Although these have been less extensively sampled, they could represent biomasses several times higher (Miller et al. 1996) than indicated in the maximum values (15 to 20 μg chlorophylll *a*/gram) 70 to 100 m from the beach observed by Ray (1989) in July and August samples.

As demonstrated at Cape Henlopen, ground water seeps are known to host varied and productive benthic communities (Kohout and Kolipinski 1967; Johannes 1980) though there is no recent ecologically comprehensive treatment of this phenomenon. This ecological response is likely the result of several effects acting simultaneously, including localized regions of greatly reduced salinity, stabilized temperature, increased nutrient flux, and resulting high microalgal abundance. The presence of *M. viridis* at Cape Henlopen apparently reflects positive factors for growth and persistence in an otherwise inhospitable environment.

Seeps as Unique Habitats/ Hydrological-Ecological Interactions

We will use our study site, Cape Henlopen, as a case study for the discussion of the ecological impacts and consequences of ground water seepage. We first consider habitat-related effects, including lowered salinity, buffered temperatures, and increased sediment stabilization by microalgal mats. Next, elevated nutrient flux is introduced in light of the possibility of eutrophication, contrasting the response we see at seeps with that described in the literature for anoxic water bodies. Finally, in the last section of this paper, we consider the trophic role of nutrients derived from ground water seepage.

Seeps at Cape Henlopen are a brackish water habitat in a euhaline, fully marine environment. In this fundamental ecological role, seeps are indeed subterranean estuaries (Moore 1999) in an ecological or habitat sense, as well as a biogeochemical one. These microestuaries have horizontal dimensions of tens of meters cross-shore to a meter or even much less (Figures 2 and 3) and vertical salinity gradients across just several centimeters in depth (Miller 1996 unpublished observations). These salinity differences equal or exceed those found over many meters vertically or hundreds of kilometers horizontally in estuaries such as the Delaware Bay (Kawabe et al. 1988). There is qualitatively apparent and quantitative (Figure 4) evidence of a close association of the seeps and dense patches of the red gilled mud worm, *M. viridis* (Figure 4), and because of their burrowing ability, we suggest that deep tube construction focuses and maintains ground water discharge in certain locations as seen in Figure 3b. This hypothesis is being studied with additional field sampling and direct sediment permeability measurements.

M. viridis has in fact been introduced into northern Europe and is considered an invasive species in the region (Atkins et al. 1987; Gruszka 1991; Lagzdins and Pallo 1994; Bastrop et al. 1995; Zettler et al. 1995; Kube et al. 1996; Zettler and Bick 1996; Röhner et al. 1996; Bastrop et al. 1997). A thorough summary of the introduction, reproduction, and physiology of *Marenzelleria* in European waters was published in 10 papers in Volume 31, Issue 2 of the journal *Aquatic Ecology* (1997). In the concluding paper of that special issue, Zettler (1997) presented a bibliography of *Marenzelleria* species and its synonyms totaling 236 publications from studies in northern Europe, the Arctic, and North America.

Recent population genetic studies of *Marenzelleria* by European authors reveal there are at least two morphologically very similar species of *M. viridis* (Bick and Zettler 1997; Bastrop et al. 1998) and that both genetic types, or sibling species, are present in Europe (Bastrop et al. 1997). Type I animals range from Cape Henlopen north to Nova Scotia and also in the North Sea. Type II from the Baltic Sea corresponds to animals from Arctic Canada, New Hampshire, and south from Chesapeake Bay to Georgia. These populations are reported to differ in their salinity preference (Bastrop et al. 1997; Bastrop et al. 1998) with Type I preferring salinities > 16 as compared with < 10 for Type II. Our observations presented here suggest that the pore water salinity of the Type I population at Cape Henlopen may be well below that indicated in the literature (Bastrop et al. 1995). Although the Cape Henlopen population has been determined to be Type I, we find worms there in abundance over the full range of salinity at the site depending on season and exact location on the sandflat (Figures 3 and 4). We cannot exclude the possibility that both Types I and II inhabit our sampling transect (Bick and Zettler 1997), but we feel it is more likely that the clear distinctions drawn in the literature in terms of salinity tolerance may as yet be tentative. The extent to which a similar proviso applies to the other, high salinity Type I populations is unknown. While Types I and II are clearly distinct genetically (determined by two independent methods, allozyme polymorphisms and mitochondrial RNA markers), their adaptations to salinity may not yet be fully understood. In addition, the degree to which the species' spread in northern Europe has been facilitated by seeps (as well as the extent to which they may be present) is not known.

At Cape Henlopen, at least, the relationship of *M. viridis* and seeps suggests that this species could serve as an indicator organism for submarine ground water discharge, although its utility may depend on local conditions. In truly oligohaline or mesohaline reaches of an estuary, ground water discharge may reduce salinity below what this species can accommodate. In such settings, absence may indicate strong seepage, and this may account for the low abundances of *M. viridis* that we found in preliminary sampling at another estuarine site (in a harbor near Roosevelt Inlet, west of Cape Henlopen). In a related habitat issue, seeps may provide corridors or stepping-stones for an upper bay species to expand its range seaward or to allow new or invasive species to become established in an area.

In addition, seeps may provide a buffered, oligohaline regime within regions of large, tidally driven salinity fluctuations. The importance of salinity in controlling distributions of organisms in estuaries has long been recognized, and fluctuations in salinity are certainly a major determinant of benthic distributions (Gage 1974; Knox 2001). Even in the experimental studies of Sanders et al. (1965), large variations in overlying salinity led them to conclude that infauna were subject to less physiological stress than epifauna due to this buffering effect (Riedl et al. 1972). Although Figure 3 does show seasonal variations in pore water salinity, especially at midtransect (12 to 14 m from beachface), reduced salinity variations could provide a more favorable osmotic environment and reduced physiological stress for organisms (Fritzsche and von Oertzen 1995), as well as having positive effects on development (George 1966; Bochert et al. 1996) especially at critical life stages.

Seeps should also be influenced by the relatively constant temperatures of source ground waters (Wehmiller et al. 2000) and provide a stabilized temperature regime for their inhabitants. While we did not measure temperature in our well sampling, we expect that sediment temperature in seeps varies less than surrounding areas on an annual basis. Such temperature differences were exploited to interpret our thermal imaging, and we have often observed in the field, while digging out benthic cores in warmer month sampling, that seep zone sediments are distinctly colder by touch than surficial sediments or tide pools. Conversely, in winter many of these seepage zones remain ice-free. In addition to the positive physiological and developmental effects (cited previously), temperature extremes have important consequences for benthic populations. Sardá et al. (1995a, 1995b) concluded that harsh, freezing winter temperatures resulted in lower abundance of *M. viridis* and other macrofauna at their marsh sites. Our observation at Cape Henlopen, which only experiences ice coverage of Breakwater Harbor about once a decade, is that *M. viridis* is abundant throughout the year.

Microalgae are widely known to control sediment stability where they occur in high abundance or even surficial mats (Wiltshire et al. 1998; Sutherland et al. 1998a, 1998b; Blanchard et al. 2000; Lucas et al. 2000; Yallop et al. 2000). Diatom cells and exopolymers surround sediment grains and bind them into a layer that resists erosion. Under high flows or direct mechanical disruption, this layer tends to peel away from unbound sediment beneath the carpet (Miller et al. 1996). In addition to the sediment becoming more cohesive in areas covered by the mat, we have observed that bubbles within the sediment (Figure 5) can make the surficial layers sponge-like with little mechanical strength (Sutherland et al. 1998b). Such effects on stability of the sediment (both positive and negative) will strongly influence sediment movement and fluxes of organic material. These fluxes have been shown to have important consequences for the sandflat macrofauna. Ray (1989) concluded that local microalgal growth was not sufficient to balance grazing by *M. viridis* and that horizontal transport was needed to meet consumption demands over the sandflat. At a smaller scale, Bock and Miller (1995) found that chlorophyll was depleted in feeding areas of individual polychaetes during calm conditions, while no such deficit was seen following sediment transport by storms.

Increasing nutrient input, typically anthropogenic in origin, is frequently suggested as a major reason for low bottom water oxygen concentrations (Diaz and Rosenberg 1995). Hypoxia (defined as < 2 mg/L dissolved oxygen) occurs commonly in fjords, estuaries, coastal bays, on the continental shelf off the Mississippi River, and in the Black Sea (Gray et al. 2002). The best-studied system in North America, Chesapeake Bay, experiences recurring seasonal hypoxia in the mesohaline regions resulting in declines in abundances of larger, long-lived benthic species in favor of dominance by smaller, short-lived species (Dauer et al. 1992). Tributaries of the Chesapeake experience intermittent hypoxic events, lasting from days to weeks and occurring at various times of the year. The ecological consequences of hypoxic events are varied: in some cases largely determining patterns in abundance and benthic species composition (Llansó 1992), while at others, benthic communities are relatively unchanged by hypoxic events (Dauer et al. 1992). Specific effects of hypoxic events reported by Dauer et al. (1992) include lower species diversity, lowered biomass, and lower proportion of deep-dwelling biomass (below 5 cm depth in sediment). Associated changes in the benthic community were seen in higher dominance of opportunistic species (euryhaline annelids) and lower dominance of equilibrium species, including long-lived bivalves.

The habitat of the seeps is one of high nutrient input. Ullman et al. (2003) concluded that beachface discharge derives from a mixture of shallow oxic surface water and a deeper upland aquifer (both of which have elevated nitrogen concentrations, 10 to > 100 μM dissolved inorganic nitrogen), in addition to water pumped by tides (and waves) into the beachface (which is nutrient poor, < 5 μM dissolved inorganic nitrogen). In terms of nutrient discharge, they report fluxes of 0.3 to 1.6 mol nitrogen and 0.03 to 0.16 mol phosphorus per meter of shoreline per day; the significance of these rates is addressed later in the paper. Note, however, that the benthic community we see at Cape Henlopen is not typical of nutrient-enriched situations, and high nutrient flux here may not be detrimental. Although the *Marenzelleria* community of the seeps is much less diverse than that nearby (Muir 2002), *M. viridis* is an annual, relatively large, and deep-dwelling species. At Cape Henlopen, the overlying water is strongly flushed tidally (and the sandflat exposed subaerially twice a day) and large amounts of macroalgae are not found because there is little substratum for attachment. Smothering of the seafloor by dense mats of benthic macroalgae may also cause anoxic conditions and severe (if species selective) impacts on benthic communities (Norkko and Bonsdorff 1996a, 1996b). *Marenzelleria* Type I populations are reported to be tolerant of low oxygen and high sulfide (Schiedek et al. 1997), and the larvae also show wide tolerance to salinity and oxygen variations (Fritzshe and von Oertzen 1995). While understanding physiological responses is important, physical factors such as runoff, wind mixing, and tidal flushing are the major controls on the timing and magnitude of hypoxic events (Gray et al. 2002). Thus understanding how the situation of ground water seeps differs in its response to eutrophication will require a more complete understanding of the recruitment and demographics of dominant species, bioturbation, burrow irrigation, tidal flushing, and biogeochemistry, and the establishment of food web relationships for this community.

Trophic Role of Ground Water–Derived Nutrients

There is a second, trophically mediated set of ecological consequences of submarine ground water seepage. Ground water discharge in the seep zone provides nutrient replete conditions. These ground water-derived nutrients may fuel production by microalgae, which may be consumed by deposit-feeders (primarily *M. viridis*), which in turn may be prey for crabs, bottom-feeding fish, and migrating shorebirds. In this way, nutrients from upland or local marine sources may foster biological productivity and diversity of a wide range of organisms. It is worth mentioning here that ground water nutrients may contribute to productivity of salt marsh halophytes (Page 1995) and seagrass (Kamermans et al. 2002), although neither of these is in much evidence at Cape Henlopen.

The key trophic link, consumption of microalgae by sandflat macrofauna, has been documented by previous studies at the Cape Henlopen seepage site. Ray (1989) attributed lower microalgal biomass (relative to offshore) in the *Marenzelleria* zone to grazing by this deposit-feeder. Bock and Miller (1995) demonstrated depletion of microalgae in individual *M. viridis* feeding pits under calm conditions at the sandflat. In laboratory experiments, Karrh and Miller (1994) showed grazing on sediment microalgae by acorn worms, another important deposit-feeder of the sandflat in nonseep locations.

Since seepage occurs in a relatively narrow zone along a wide extent of beachface, it is reasonable to estimate biological productivity and nutrients required to support it per meter width of beachface, integrating over the first 20 m from the beachface seaward (Figure 3) (Ullman et al. 2003). We do not have field primary productivity values from the seep zone, and these are challenging measurements to make under the best circumstances. Taking values from MacIntyre et al. (1996) for sites of similar microalgal biomass and latitude, we estimate productivity of 1 g $C/m^2/d$, recognizing that there is severalfold variability about this rough figure for these literature values (Knox 2001). For each meter of beachface (i.e., area extending 20 m seaward), the areally integrated primary productivity is 20 g C/m/day or 1.7 mol C/m/day. Converting this to a nitrogen basis using a C:N ratio for fresh marine organic matter (6.25) yields an estimated demand of 0.27 mol N/m/day. The demand is approximately one-half to one-tenth the total nitrogen flux measured for this sandflat (4 to 17 mol C/m/day or 0.6 to 2.7 mol N/m/day [Ullman et al. 2003]). Thus, it is clear that even if this nitrogen flux is a seasonally elevated value (Ullman et al. 2003) and the productivity of the algal mat has been underestimated (Figure 5), it seems reasonable to conclude that microalgal productivity can be fully supported by ground water-derived nutrients.

This analysis assumes uniformity in all spatial directions and over time, and our field survey and transect data clearly show that this is only a rough approximation. Aside from impacts local to the seeps themselves, other effects may be difficult to demonstrate at Cape Henlopen because it is open to the Delaware Bay and well flushed by tides. This contrasts with what we might find in smaller and more restricted embayments and lagoons where, as a first approximation, we would expect nutrient-driven effects for the bay as a whole to scale roughly as a shoreline perimeter to bay volume ratio. This purely geometric effect would be greatest for small bays and be magnified by restrictions on tidal flushing. The longer hydrodynamic residence of dissolved nutrients should make them more accessible to algae and higher plants (Page 1995; Kamermans et al. 2002), and ecological impacts may be relatively more dramatic than at larger and more hydrodynamically open sites.

Since *M. viridis* abundances at Cape Henlopen are similar to those reported by Sardá et al. (1995b), it is possible to estimate secondary productivity and, ultimately, nutrient flux needed to meet that rate. However, this is a less direct calculation than that made previously, and it is important to note that biomass and productivity can be seemingly decoupled in annual species reproducing once a year. It is more instructive to examine the population demographics and productivity as they relate seasonally to seepage and nutrient fluxes. In our March 1998 core samples, we found that small *M. viridis* were present in samples and extended even to the seaward end of the transect. This cold season recruitment at Cape Henlopen is consistent with that which has been reported by George (1966) for Nova Scotia populations and Sardá et al. (1995b) for New England sites, as well as that summarized for Type I populations in Bick and Zettler (1997) and Bochert (1997). As noted previously, recruitment of *M. viridis* at Cape Henlopen occurs in the cold months of the year, coincident with the expected and observed maximum extent of seepage (Figure 3b), and this may be advantageous to colonization and expansion of the Cape Henlopen populations.

Sardá et al. (1995b) report a striking drop in *Marenzelleria* population density through the summer at their site, which was attributed to competition for food resources and predation (Sardá et al. 1998) or potentially emigration (Essink and Kleef 1993). While we observed a decrease in abundance between June and September (Figure 4), the population was considerably more stable at Cape Henlopen than that in New England documented by Sardá et al. (1995b), falling from peaks > $10{,}000/m^2$ to ~$2{,}000/m^2$ in fall. It is tempting to speculate that the Cape Henlopen population is sustained through this time by seasonally high nutrient flux and microalgal productivity. Further, late growing season productivity and accumulation of biomass in anticipation of overwintering and reproduction may be promoted by ground water-derived nutrients. George (1966) found that Nova Scotia populations of *M. viridis* showed no gamete production until October, increasing rapidly to over half the females (and almost all of the males) within two months.

While it is unclear if the exact reproductive timing of this northerly population applies to that at Cape Henlopen (as it should based on its Type I classification [Bick and Zettler 1997; Bochert 1997]), clearly the late growing season is an important time in the breeding cycle and the *M. viridis* reproductive potential may benefit directly from the enhanced ground water discharge and nutrient flux (Ullman et al. 2003) seen at this time of the year.

Conclusions

Thermal imaging in the lower Delaware Bay shows that ground water seepage is most apparent on the sandflats in Breakwater Harbor adjacent to Cape Henlopen. On-site sampling confirmed that seepage occurs widely along the shoreline in this region of the bay within 20 m of the beachface, and that interstitial salinities and presumably seepage rates varied in a repeatable seasonal cycle. Within this narrow region, discharge was extremely variable at the 1 m scale and closely associated with patchy, high abundances of the red gilled mud worm. The life cycle of this benthic polychaete, which is typically characterized as an oligohaline estuarine species, is correlated with the seasonal cycle in seepage, and this suggests a role in providing suitable habitat in an otherwise unsuitable location. High nutrient discharge and the presence of a microalgal mat suggests other roles for discharge in terms of sediment stability, increased food supply, and elevated productivity and benthic biomass. A simplified analysis of the food web suggests that these seeps may have an ecological role substantially greater than their relative area or water discharge rates suggest. In particular, red gilled mud worms may be a key trophic linkage between microalgal growth fueled by high nutrient loads associated with the discharging ground waters and worm-feeding predators such as bottom fish or shorebirds common on the Cape Henlopen sandflat.

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